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THE RELEVANCY OF THE GENERIC CONCEPT TO THE GEOGRAPHIC DISTRIBUTION OF LIVING OYSTERS (GRYPHAEIDAE AND OSTREIDAE)

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ABSTRACT

Since 1758, numerous species of living oysters have been named, mostly in the genus *Ostrea*. Beginning in the 1930's, more extensive anatomical investigations resulted in the acceptance of more genera, improved definition of taxa, and a great reduction in the number of accepted specific names. Presently the 36 recognized species are distributed among 24 genera and subgenera. These species are so distributed geographically that only one species of a genus (or subgenus) occurs in a given area. An area is here defined as one latitudinal climatic zone of a province, the latter being longitudinal regions of shallow water separated alternately by continental masses and broad areas of deep water. As now restricted, genera consist of either two or more allopatric species, or a single species so distinct that it does not have a geminate species in another area. These morphological and distributional limits of genera are probably valid for other shallow water benthic marine mollusks, few groups of which have had exhaustive generic analysis based on extensive comparative anatomical studies within a family.

The taxonomic history of molluscan genera which were introduced in the 18th century can usually be divided into three stages. In the initial stage, a genus was introduced, with few to many species; there was no conscious recognition of types, nor families or other categories between genus and order. The second stage was one of generic expansion, during which many additional species were named in each of the few recognized genera. More categories and the type concept were introduced, usually with vague application. The third stage was one of generic analysis and restriction; the number of genera was increased, but now each had only one or a few species; the type concept was more rigorously applied. Several more categories were introduced, including suborder, superfamily, tribe and subgenus. The taxa were more precisely defined through extensive comparative anatomical studies, distribution and behavior.

The taxonomic history of oysters exemplifies these stages very well (Table 1). When Linné (1758) proposed a list of oysters in the tenth edition of the Systema Naturae, he included several species of bivalves in the genus *Ostrea* which would not be considered true oysters today, and some of the true oysters that he first described he put in the genera *Mytilus* and *Anomia*.

Other authors of the late 18th century (e.g. Born, 1778; Gmelin, 1791) continued to use the system of Linné, introducing new species of oysters in the genus *Ostrea*. In the early part of the 19th century Lamarck (1815-1822) made important revisions in the system of Linné. In the case of oysters, he removed several groups from *Ostrea* to other genera, notably *Pecten, Malleus, Placuna*, etc., and he transferred the species of oysters which Linné had put in other genera to *Ostrea*. He also named many new species in that genus. For the rest of the 19th century authors continued to add to the list of oysters, nearly always placing the new species in the genus *Ostrea*. Other genera were introduced, but not widely used, and none had its limits well defined anatomically.

There was an intensified interest in oyster systematics during the 1930's, with several authors approaching the subject in different ways. Lamy (1929-1930) compiled and evaluated the nominal species of oysters which had been proposed; Orton (1928) stressed the distinction between those oysters which are larviparous and those which are oviparous, and Nelson (1938) showed that there is a major morphological difference between the two groups; Vyalov (1937) introduced several new genera and subgenera, and recognized four subfamilies (two extinct), but his proposals were not immediately accepted; instead, the influence of Ranson (1943) prevailed, and all living species were distributed among three genera, in one family, without subfamilies or other divisions: *Pycnodonte, Ostrea* and *Crassostrea*. Several papers of the

Table 1. Summary of the conceptual history of classification of the oysters, families Gryphaeidae and Ostreidae. The names of authors in the top row indicate those most responsible for the developments in generic expansion at the time below their names, and the dates. At the bottom of the table the general state of taxonomic procedure is indicated, as exemplified in the work of the authors cited.

HISTORY OF GENERIC EXHAUSTION IN TRUE OYSTERS (GRYPHAEIDAE AND OSTREIDAE)

Linnaeus	Lamarck	Lamy Nelson Orton Ranson Vyalov	Stenzel	Torigoe Harry
1758	1819	1930's	1971	1981- 1985
OSTREA (Included true oysters plus many others) *MYTILUS* (Included three true oysters *ANOMIA* (Included one fossil oyster)	*OSTREA* (Genus limited to true oysters; those in *MYTILUS* also placed here)	*OSTREA* *CRASSOSTREA* *PYCNODONTE*	*HYOTISSA* *NEOPYCNODONTE* *OSTREA* *SACCOSTREA* *STRIOSTREA* *CRASSOSTREA* *LOPHA* *ALECTRYONELLA* *(ANOMIOSTREA)*	*HYOTISSA* *PARAHYOTISSA* *P. (PLIOHYOTISSA)* *P. (NUMISMOIDA)* *NEOPYCNODONTE* *LOPHA* *ALECTRYONELLA* *DENDOSTREA* *MYRAKEENA* *ANOMIOSTREA* *OSTREOLA* *OSTREA* *O. (EOSTREA)* *NANOSTREA* *PLANOSTREA* *CRYPTOSTREA* *TESKEYOSTREA* *BOONEOSTREA* *PUSTULOSTREA* *UNDULOSTREA* *SACCOSTREA* *STRIOSTREA* *S. (PARASTRIOSTREA)* *CRASSOSTREA*
NO FAMILIES NO SUBFAMILIES NO TRIBES NO SUBGENERA	ONE FAMILY NO SUBFAMILIES NO TRIBES NO SUBGENERA	ONE FAMILY NO SUBFAMILIES NO TRIBES NO SUBGENERA	TWO FAMILES FIVE SUBFAMILIES (2 extinct) NO TRIBES (in living Oyst.) NO SUBGENERA	TWO FAMILIES FOUR SUBFAMILIES TEN TRIBES SUBGENERA RECOGNIZED

next three decades adopted that system (Thompson, 1954; Galtsoff, 1964); however, the authors of faunal catalogues were more conservative, referring nearly all living oysters to the single genus *Ostrea* (McLean, 1941; Olsson, 1961; Keen, 1971).

Stenzel (1971) made a major revision of the systematics of oysters and attempted to unify the subject by extending the generic analyses to both fossil and recent species. He accepted numerous genera proposed by Vyalov and earlier workers, besides proposing a few himself, and he recognized two families and five subfamiles (two extinct). He distributed the living oysters among nine genera (Table 1). However, only the type species were considered in any detail by Stenzel, who illustrated and described them extensively, with strict application of the type concept.

Therefore there remained the problem of allocating all other living species of oysters, which are not types of genera, to the genera which he recognized. A first step was to use the more reliable faunal lists of selected areas, such as those of McLean (1941) for the Western Atlantic, and Olsson (1961) and Keen (1971) for the Eastern Pacific. The process was augmented by studying the extensive collection of oysters at the U.S. National Museum of Natural History, the British Museum of Natural History, the Houston Museum of Natural Science and several large private collections. Studying the flesh of oysters, as well as more careful attention to shell characters, resulted in more exact definitions of taxa. Several new taxa were recognized, at the level of subgenus, genus, tribe and subfamily, to explain the relationships and diversity of oysters more exactly (Harry, 1985).

Torigoe (1981), whose study was limited to the living oysters of Japan, independently found several new anatomical characters which are useful in systematics. He named one new subfamily, Crassostreinae, but no taxa at lower levels.

From the standpoint of faunal distribution of the taxa, it soon became evident that every species of a given area belongs to a different genus or subgenus; or, by logical conversion of this proposition: a genus or subgenus is represented in a given area by only one species. This does not preclude the possibility of a species extending into more than one area, and indeed it implies that genera may do so. The principle will be more easily understood if we understand the meaning of the terms genus and area, as they are used here.

In studying the distribution of shallow water benthic marine molluscs, six major regions are generally recognized (Fig. 1). Four are longitudinal, and these we may call provinces: Eastern Atlantic, Western Atlantic, Eastern Pacific and Indo-Western Pacific. The two latitudinal regions, which we may call zones, are the Arctic and Antarctic. The natural boundaries of these provinces and zones are formed by things which constitute distributional barriers, and they are of three kinds. The longitudinal barriers are alternating continental masses and broad areas of deep water. The two latitudinal zones are separated not only by great distance, but also by temperature gradients along the provinces.

The provinces can be subdivided by regimes of light and temperature variation, and these might be exactly limited by the Arctic and Antarctic Circles and the Tropics of Cancer and Capricorn, except for the presence of major oceanic currents. Around Antarctica the water moves in a single current, from west to east; it is uniformly cold, throughout the year. No comparable current serves as a barrier in the Arctic Ocean, where the shallow water region is along the northern shores of Eurasia and North America, and the ocean is separated from the others by a narrow passage into the Pacific and a broader one into the Atlantic Ocean. In

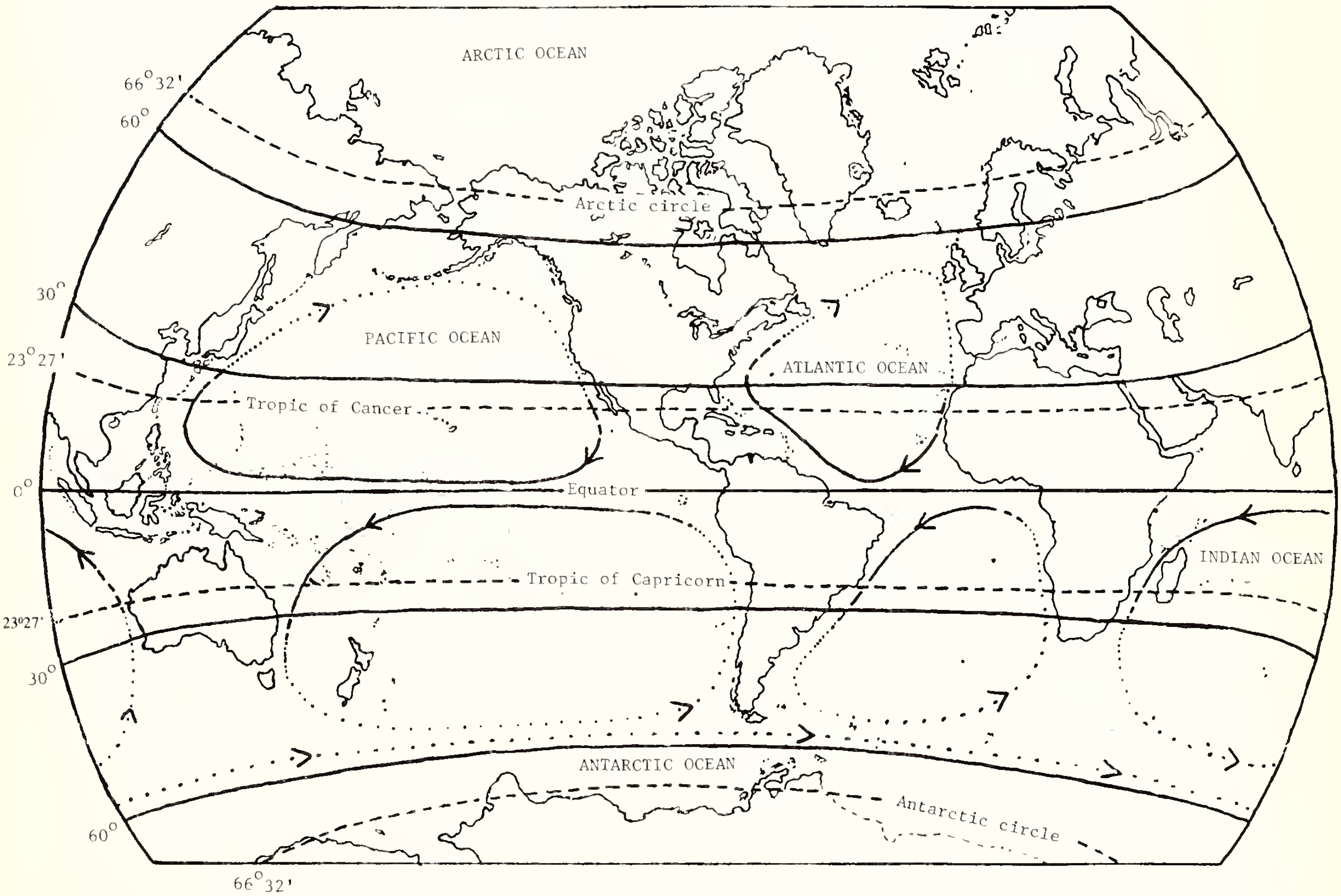

Fig. 1. Map of the world, showing the latitudes bounding climatic zones (labeled: Arctic and Antarctic Circles, Tropics of Cancer and Capicorn), and the effect of major ocean currents in shifting the real thermal boundaries of those zones. Arrows on the lines indicating oceanic currents show direction of movement; continuity of those lines indicate temperature; the continuous part of each line representing the warmer part of a current, with the cooler part being dotted.

temperate and tropical latitudes, the major ocean currents form large gyres. They take up heat in the low latitudes, and release it gradually in higher ones. Thus they act as giant heat distributors, because water heats and cools more slowly than air or land. The gyres distort the climatic zones on all continental coasts. In the northern hemisphere the gyres move clockwise, whereas those of the southern hemisphere move in the opposite direction. Consequently the climate of a given latitude in the temperate zones is warmer on the eastern than on the western margin of a continental mass.

The range of temperature in which each species occurs varies with the species, and it is impractical, for present purposes, to define the subzones of the provinces precisely; these subzones are, from north to south: Northern Cool Temperate, Northern Warm Temperate, Tropical, Southern Warm Temperate and Southern Cool Temperate. An area, for purposes of applying the principle stated above, is one climatic zone of a province.

The distribution of the 36 species of living oysters which I can presently recognize are shown in Table 2. No species occurs in the Arctic or Antarctic zones, which are therefore omitted.

All genera but one are represented in the tropics. One species, *Neopycnoconte cochlear* (Poli, 1795) is nearly world wide in distribution, although localized and infrequently taken; this reaches the greatest depth of any oyster, 2100 m, and although it has been found as shallow as 27 m, a depth attained and exceeded by a few other species, most of the records of this oyster are from below 200 m, a depth not reached by other species. It has not been found in the Eastern Pacific province. A shallow water species, *Ostrea (Eostrea) puelchana* Orbigny, 1846, is also world wide, but will be dealt with below.

Several species of oysters occur in two adjacent provinces, as follows: *Hyotissa hyotis* (Linné, 1758) in the Indo-Western Pacific and Eastern Pacific; *Parahyotissa mcgintyi* (Harry, 1985) in the Western Atlantic and Eastern Atlantic; *Dendostrea frons* (Linné, 1758) in the Western Atlantic and Eastern Atlantic; and *Saccostrea cucullata* (Born, 1778) in the Eastern Atlantic and Indo-Western Pacific.

Seventeen of the 24 genera and subgenera are monotypic; excepting the three noted above, *N. cochlear, H. hyotis* and *O. (E.) puelchana,* their species are limited to one province, and often to a very small part of that province. That leaves seven genera and subgenera with species ranging from two to four in number; of these, no genus or subgenus has more than one species in a given province: *Parahyotissa, Dendostrea, Ostreola, Ostrea s. s., Saccostrea, Striostrea s. s.* and *Crassostrea*. If one examines the species of those genera and subgenera, one finds that the species are extremely similar to each other. They are what are generally called analogous species. Several other terms are used to designate this close similarity of species of different provinces, notably allopatric species, geminate or twin species, homologous species, vicarious species and cognate species.

The concept of genus in oysters probably should be restricted to analogous species as the latter are thus defined. Or, if a species has no close analogue in another province, it should be recognized as a monotypic genus (or subgenus, depending on the degree of difference from other species most similar to it). The hesitation and qualification of these assertions are deliberate, because genera and species should ultimately be differentiated on a morphological basis, to which the distinctness in distribution is secondary. Morphological differences among all genera and subgenera of oysters here recognized have been found (Harry, 1985).

Species of a few genera, notably *Ostreola* and *Crassostrea*, extend from the Tropical through the Warm Temperate and even to the Cool Temperate zones. One genus of oysters that does not live in the Tropical, or even within the Warm Temperate zone, is the genus *Ostrea* as restricted by my studies. It has only three species, but in two subgenera. *Ostrea s.s.* has two species, broadly separated; both occur in the northern hemisphere, approximately between the latitudes 35° and 60° north, on the coasts of Europe (*O. edulis* Linné, 1758) and Asia and Japan (*O. denselamellosa* Lischke, 1869). These are most abundant at several meters depth, but an occasional specimen occurs in the low intertidal area. The third species, *O. (E.) puelchana,* occurs around the world in the southern hemisphere between latitudes 35° and 50° south. It is found on both coasts of South America, the southern island of New Zealand, the southern coast of Australia, off South Africa, and at some smaller islands. Oddly, no species of true *Ostrea* as presently defined lives naturally on the coasts of North America.

Thus, genera are not present in all areas where they might be expected, on the basis of climatic preference of their species elsewhere. *Saccostrea* and *Striostrea* are absent from the Western Atlantic, but present in the other three provinces. A very interesting case is *Ostreola*. It is not present in the Indo-Western Pacific province, where two monotypic genera closely related to it occur. One is *Nanostrea*, a dwarf oyster which seems to lead to three monotypic genera placed in Cryptostreini, the species of which are small, reclusive and with reduced features. The other is *Planostrea*, which in many ways is the tropical counterpart of *Ostrea*, intermediate between it and *Ostreola*.

Is the principle of 'only one species of a genus in an area' applicable to molluscs other than oysters? A cursory examination of some of the more extensive systematic works on other families suggests that it is, at least for some. As data are accumulated, very likely some modifications or limitations of the maxim's applicability will be found necessary. One obvious limitation is the habitat of the molluscs involved. The principle may be limited in the marine environment to shallow water, benthic molluscs, i.e., those living in or near the substrate, in less than 200 m depth. This excludes pelagic and abyssal species, whose environment is more uniform, and with fewer isolation barriers.

A prerequisite for applying the principle is that an exhaustive study of the species of a family must have been made, and genera determined on the basis of extensive anatomical examination. This has been done on surprisingly few mollusc groups, especially among marine ones. Certainly few marine groups have been as thoroughly explored anatomically as the Unionidae of fresh water, and the ter-

Table 2. Systemic distribution in families, subfamilies and tribes of the living oysters are in the three columns on the left of the genera and species. On the right the distribution of each species is shown in the five climatic zones of the four provinces recognized. The provinces are: I.W. Pac - Indo-Western Pacific; E. Pac. - Eastern Pacific; W. Atl. - Western Atlantic; E. Atl. - Eastern Atlantic. The zones are: N.C. - Northern Cool Temperate; N.W. - Northern Warm Temperate; TROP. - Tropical; S.W. - Southern Warm Temperate; S.C. - Southern Cool Temperate.

FAMILY	SUBFAM.	TRIBE	GENUS AND SPECIES	I.-W. Pac.					E. Pac.					W. Atl.					E. Atl.				
				N.C.	N.W.	Trop	S.W.	S.C.	N.C.	N.W.	Trop	S.W.	S.C.	N.C.	N.W.	Trop	S.W.	S.C.	N.C.	N.W.	Trop	S.W.	S.C.
GRYPHAEIDAE	PYCNODONTEINAE	HYOTISSINI	*HYOTISSA HYOTIS* (Linne, 1758)			X					X												
			PARAHYOTISSA MCGINTYI Harry, 1985												X	X					X		
			P. IMBRICATA (Lamarck, 1819)			X																	
			P. (PLIOHYOTISSA) QUERCINUS (Sowerby, 1871)							X	X												
			P. (NUMISMOIDA) NUMISMA Lamarck, 1819)			X																	
		N.	*NEOPYCNODONTE COCHLEAR* (Poli, 1795)		X	X	X								X					X			
OSTREIDAE	LOPHINAE	LOPHINI	*LOPHA CRISTAGALLI* (Linne, 1758)		X	X																	
			ALECTRYONELLA PLICATULA (Gmelin, 1791)		X	X																	
			DENDOSTREA FOLIUM (Linne, 1758)		X	X																	
			D. FRONS (Linne, 1758)												X	X	?				X		
			D. MEXICANA (Sowerby, 1871)							X													
		M.	*MYRAKEENA ANGELICA* Rochebrune, 1895)							X													
			ANOMIOSTREA CORALLIOPHILA Habe, 1975			X																	
	OSTREINAE	OSTREINI	*OSTREOLA STENTINA* (Payraudeau, 1826)																	X	X	?	
			O. EQUESTRIS (Say, 1834)												X	X	X	?					
			O. CONCHAPHILA (Carpenter, 1857)						X	X	X	?											
			OSTREA EDULIS Linne, 1758																X				
			O. DENSELAMELLOSA Lischke, 1869	X																			
			O. (EOSTREA) PUELCHANA Orbigny, 1846					X					X					X					X
			NANOSTREA EXIGUA Harry, 1985			X																	
			PLANOSTREA PESTIGRIS (Hanley, 1846)			X																	
		CRYPT.	*CRYPTOSTREA PERMOLLIS* (Sowerby, 1871)												X	?							
			TESKEYOSTREA WEBERI (Olsson, 1951												X	X							
			BOONEOSTREA CUCULLINA (Deshayes, 1836)			X																	
		P.	*PUSTULOSTREA TUBERCULATA* (Lamarck, 1804)			X																	
		U.	*UNDULOSTREA MEGODON* (Hanley, 1846)								X												
	CRASSOSTREINAE	STRIOSTREINI	*SACCOSTREA CUCULLATA* (Born, 1778)		X	X	X													?	X	?	
			SACCOSTREA PALMULA (Carpenter, 1857)							X	X												
			STRIOSTREA MARGARITACEA (Lamarck, 1819)																		X	X	
			S. PRISMATICA (Gray, 1825)								X												
			S. CIRCUMPICTA (Pilsbry, 1904)		X	?																	
			S. (PARASTRIOSTREA) MYTILOIDES (Lamarck, 1819)		?	X																	
		CRASS.	*CRASSOSTREA VIRGINICA* (Gmelin, 1791)											X	X	X	?						
			C. ANGULATA (Lamarck, 1819)																	X	X		
			C. COLUMBIENSIS (Hanley, 1846)							X	X												
			C. GIGAS (Thurnberg, 1793)	X	X	X																	

restrial helicoid snails. A century ago the species of those two groups were nearly all put in the genera *Unio* and *Helix*, respectively, each with a very large number of species. Extensive anatomical investigations led to the large number of genera presently recognized, with relatively few species in a genus.

I have found only one other study with exhaustive generic analysis, accompanied by extensive anatomical studies, which was done on marine bivalves. That is Turner's (1966) monograph of the Teredinidae. Although the distributional correlation is not presented in a simple fashion in that paper, when extracted it fits the principle proposed above very well. The few exceptions merit further attention.

Such studies must be on a world-wide basis, in groups which have such distribution. In recent years, most systematic monographs of families of marine molluscs have been limited to one province, as defined above, but some of those cite species of the genera they treat which occur in other provinces, and even correlate analogous species among provinces. Examples are Grau (1959) on the Pectinidae of the Eastern Pacific province, and several papers in the serial monographs, "Indo-Pacific Mollusks," particularly by Abbott (1960) on the genus *Strombus* and Rosewater (1970) on the Littorinidae.

Several statements were found in the literature which support the general idea, although they do not relate the obvious implications of the principle of generic limitation on a geographic basis to systematics and nomenclature in a practical way. In a paper on the origin of species in littoral prosobranchs, Fretter and Graham (1963) noted: "It is likely that speciation in the gastropods of marine habitats has been brought about primarily by means of geographic isolation. So little work, however, has been done upon this aspect of the evolution of the group, or indeed, of any group of marine invertebrates, that this statement of probability is as far as one should go. The only study of marine gastropods with this as one of its explicit aims—that of the cypraeids by the Schilders (1939)—concluded that speciation has been primarily allopatric and that the preceeding isolation was brought about by geographical barriers. Similarly Mayr (1954) concluded that allopatric speciation has been the only significant source of new species amongst echinoids."

The noted ichthyologist and first president of Stanford University, David Starr Jordan (1905), made a statement that approximates the formulation of the principle as presented in this paper even more closely: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort."

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